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COMMENTARIES

Confusions of Mass and Size

THEUNIS PIERSMA[1] AND NICK C. DAVIDSON[2]

Work by Rising and Somers (1989) and Freeman and Jackson (1990) has recently emphasized that multiple, and preferably skeletal, measurements provide a more accurate assessment of body size in birds than do single, external measurements. We agree. It is regrettable, however, that both papers perpetrate a confusion between two useful and quite distinct variables: *body size* and *body mass*. In doing so they have ignored several highly relevant published studies, notably of nonpasserine and European species (the latter bias apparently part of a more general trend identified by Enckell 1988).

Rising and Somers (1989) and Freeman and Jackson (1990) are but two recent examples of a widespread misunderstanding. Smith et al. (1990) provide a further instance. Another is the inclusion by Davies et al. (1988) of mass in an analysis of body size of Lesser Snow Geese (*Chen c. caerulescens*), which was criticized recently by Alisauskas and Ankney (1990), although in this case the overall interpretation of a size-related variation in fecundity of Lesser Snow Geese may not have been affected (Cooke et al. 1990). Even Peters (1984), in his extensive discussion of the ecological implications of body size, provides no clear definition of body size and in many instances discusses body size-related phenomena through body mass.

Although not stated explicitly, both Rising and Somers (1989) and Freeman and Jackson (1990) addressed problems of measuring *structural size*. The Oxford dictionary defines structural as "of the (essential) framework" and structural size accordingly as "the size of the essential framework" (Piersma 1984). Because individual birds have a remarkable capacity to vary their mass and volume depending on their nutritional status, we feel it is biologically most meaningful to define structural size as the "nutrient reserve-independent size of a bird."

Our point is simple. There is an important but widely ignored distinction that must be made between two concepts: (1) the reserve-independent *structural size* and (2) the variable amounts of nutrients (chiefly fat and protein) that permit birds to exercise and to survive periods of negative energy and nutrient balance, the variable *nutrient reserve mass*. Body mass combines information about structural size and nutrient reserve mass but alone cannot provide an indicator of structural size. It is the ease with which body mass can be measured (and not the difficulty; *contra* Freeman and Jackson 1990) that has made it a much used and interesting measure. Inclusion of body mass in structural size-related analyses may not always distort interpretation of the data (e.g. see Cooke et al. 1990), but it is usually impossible to determine this from ambiguous results.

By definition structural size is independent of the nutritional status that varies with time of day and year, reproductive status, and habitat quality. For this reason structural size is the preferred variable in studies of geographical size variation and perhaps in behavioral studies of contests. Note, however, that it may not be structural size per se but rather muscular power (possibly reflected in the protein reserve mass) that determines contest outcomes. Whereas studies of geographical size variation regard all this nutritional noise as a problem to be removed, studies of energetics and nutrient reserve status require precisely this information on reserve mass. For such studies body mass can be a useful variable if mass variations due to differences in structural size can be controlled (e.g. Davidson 1983, Ankney and Afton 1988, Piersma 1988, Piersma and van Brederode 1990).

Although body mass is readily measured, structural size is more difficult, and there have been surprisingly few attempts to devise practical means of measuring structural size in birds. One approach is to define structural size as the body mass of starved birds (i.e. birds that have died after exhausting all their nutrient reserves [Piersma 1984, 1988; see King and Murphy 1985 for the distinction between nutrient *reserves* and nutrient *stores*]) and then see which body dimensions statistically "explain" starved body mass most accurately. There are, however, pitfalls even in this approach. Although birds die in natural starvation events after substantially depleting their fat and protein reserves, there is evidence that the precise nutritional state at death is influenced by the environmental conditions during starvation. This can lead to both the fat mass and the nonfat mass of starved birds still including some nutritional reserves, although absolute amounts are small (Davidson and Evans 1982, Davidson and Clark 1985).

Skeletal measurements of the sternum have been used to index pectoral muscle size (Evans and Smith 1975, Piersma et al. 1984), but these linear measurements cover only part of the overall skeletal size. As suggested by Wishart (1979), (dry and fat-free) skeletal mass is almost entirely reserve-independent, ex-

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cept for small variations in bone marrow mass (see Moser and Rusch 1988), and should provide an accurate estimator of structural size on which linear dimensions can be regressed to provide an index of structural size. Moser and Rusch (1988) concluded that skeletal volume, measured by water displacement of excised bones, provides an even more precise measure of structural size. Finally, the first principal component of a set of linear skeletal measurements likewise provides an appropriate structural size measure (Ankney and Afton 1988, Rising and Somers 1989).

Most skeletal measurements require the sacrifice of birds and are of little help in studies of live birds. Consequently, body-size variation in live birds is usually controlled in analyses of body mass by the use of one or more easily measured external measurements, typically the lengths of wing, tarsus, body, and bill. Choice of the appropriate external dimensions to indicate structural size can be made with appropriate models of regression on starved or skeletal mass or volume, as outlined above, and their derivation may hold some surprises. For example, Moser and Rusch (1988) found that some commonly used external measures were only moderate correlates of structural size (measured by skeletal volume) in Canada Geese (*Branta canadensis*). Further, the most appropriate external measures may differ interspecifically, even between closely related species (e.g. in *Podiceps* grebes, Piersma 1988).

Future studies must differentiate clearly between structural-size and nutritional-mass variation, and should avoid using body mass in exercises aimed at describing structural size. Failure to distinguish between the two can lead to ambiguous and misleading interpretations. For example, the regional differences in flight-surface loading of *Accipiter* hawks described by Smith et al. (1990) may be purely structural and adaptively related to differences in the relative use of thermal updrafts, as the authors suggest, or they may be a consequence of differences in fat-reserve mass in relation to the length of the ensuing nonstop flight (see e.g. Smith et al. 1986).

Although easy to define in general, structural size defies a uniform approximation in terms of a standard set of external measurements and should preferably be derived for each species under study. Clearly, there is still much to be elucidated about the relationships between structural size and body mass, but the unjustifiable inclusion of body mass in analyses of structural size only serves to confuse interpretation of phenomena such as nutrient-reserve storage and geographical-size variation.

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On the Use of Tape Recorders in Avifaunal Surveys

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The utility of tape recorders and tape playbacks for censusing birds is widely recognized (Johnson et al. 1981), but little emphasis has been placed on their importance in faunal surveys. Tape recorders are indispensable for finding rare, secretive, or patchily distributed species, and for documenting the composition of mixed-species flocks in forest canopy. Awareness of vocal differences in the field and taping has led to the discovery of several taxa new to science (Parker and O'Neill 1985, Parker and Schulenberg MS), and to the recognition of numerous species previously considered subspecies (Lanyon 1967, 1978; Pierpont and Fitzpatrick 1983).

One person equipped with a tape recorder and directional microphone can document a surprisingly high percentage of a tropical forest avifauna within 4–7 days during the proper season. Without tape recorders, several weeks (or even months) are required to locate most of the resident bird species in any lowland Amazonian locality, and such an effort would involve a large number of experienced observers using the best optical equipment and many mist nets.

On a recent Louisiana State University Museum of Zoology (LSUMZ) expedition to the Department of Pando in Amazonian Bolivia (Parker and Remsen 1987), I tape-recorded 243 species found within an area ca. 2 km^2 of upland rain forest in only seven days. The "final" list of forest birds for the same area, after 54 days of intensive fieldwork (including 36,804 mist-net hours) by seven experienced ornithologists, included 287 species. I tape-recorded 85% of the avifauna in just one week. Ten of the species that I missed altogether were almost certainly visitors to the site, and most of the other species not found were those typically missed during brief surveys of rain forests, such as forest raptors and canopy hummingbirds.

In an age when few ornithologists collect specimens, taping is the quickest and most practical way to build an inventory of a diverse avifauna. Locality lists based only on sight records should be viewed with some skepticism (and are likely to be far from complete). I urge conservation organizations that fund avifaunal surveys in tropical forests around the world to *require* their recipients to use tape recorders systematically. Copies of all recordings should be placed in a professionally maintained sound collection that provides easy access to researchers. Survey budgets should include travel funds for investigators to visit a sound collection before or after an expedition, and funds for sound specialists to identify or verify recordings. Those unprepared to deal with bird-song identification in the tropics are simply wasting valuable, limited research funds that could better be spent elsewhere.

Fortunately, relatively few Neotropical bird songs remain unrecorded. The Library of Natural Sounds at Cornell University contains recordings of songs or calls of 671 of the approximately 770 resident forest birds found within Amazonia below 1,000 m, or 87% of the richest avifauna on earth! Other collections, such as those in the Florida State Museum Bioacoustical Laboratory (Gainesville, Florida, USA), the Arquivo Sonoro Neotropical (Universidade Estadual de Campinas, Campinas, Brazil), and the Laborotorio de Sonidos Naturales (Museo de Ciencias Naturales, Buenos Aires, Argentina), contain recordings of many additional Neotropical species. Because field ornithologists associated with these institutions can identify the majority of bird voices recorded in the Neotropics, they can greatly facilitate the compilation of locality lists from tapes.

The following guidelines will enhance one's chances of compiling an accurate locality list in a tropical forest:

1. Get up well before dawn and be out in the area to be surveyed at least 15 min before first light. Many Neotropical species (especially tinamous, puffbirds, woodcreepers, and flycatchers) sing only 1–3 songs during the first 5 min of light (often well before light enough to see), and they rarely vocalize thereafter, until an even briefer period late in the day. Nocturnal species often call just before

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